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ECOLOGY

Release of Macronutrients from Decomposing Litter in *Pino-Quercetum* and *Carici elongatae-Alnetum* Associations. The Role of Litter Microorganisms and Saprophages in Releasing Processes

by

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Summary. Some patterns in the release of macronutrients (C, N, Ca, Mg, K, P, Na) from litter are analysed for two types of ecosystems: *Pino-Quercetum* with litter poor in nutrients, and *Carici elongatae-Alnetum* where litter contains many nutrients. The average rate of nutrient release in the oak-pine forest appeared to be considerably lower and less regular than in the alderwood. In the former ecosystem some nutrients, such as K and Mg, are very rapidly released, others are slowly released, and some of them, such as N, Ca and Na, are even accumulated over the year. This phenomenon is determined by the character of the activity of litter microorganisms which accumulate N, Ca and Na when the falling organic matter is scarce in nutrients and inhibit the accumulation when it is rich in nutrients. On the other hand, the saprophages which initiate and speed up the release of a number of nutrients (N, Ca. P, C) are considerably less active in the detritus food chain of the oak-pine forest, than in the alderwood.

The chemical composition of falling organic matter in forest ecosystems can largely be modified by plants due to the differences in the rate of autumnal withdrawal or accumulation of nutrients [4, 7—9]. The present paper characterizes some patterns of the release of macronutrients (C, N, Ca, Mg, K, Na and P) from the litter of two ecosystems with extremely different nutrient utilization. These are an oak-pine forest with poor litter, where nutrients are withdrawn at a very high rate, and a wet alderwood, where the rate of withdrawal is low and litter is rich in nutrients.

The study was carried out in the Kampinos National Park, in 1973—1974. Two types of forest communities were selected: an oak-pine forest *Pino-Quercetum* and the terrestrial part of a wet alderwood *Carici elongatae-Alnetum*. They were situated on loose sands.

New modifications were introduced to the methods for the estimation of the rate of nutrient release from litter. First, the standard method of nylon bags was replaced by the technique of glass filtres introduced under the soil which are permeable for solutions and retain all morphic particles. Due to this it was possible to calcu-

late a detailed annual balance for particular nutrients over the annual cycle of litter decomposition taking into account also the faeces of saprophages which were underestimated by the litter bag method. Secondly, the calculation technique of the rate of nutrient release from litter was modified; losses or gains in the amount of a nutrient were measured at successive time periods per 1 cm^2 of litter (the surface area of a dead leaf). These modifications made it possible to calculate a number of important parameters, such as detailed quantitative dynamics both release and accumulation of nutrients in morphic litter, the role of microorganisms and saprophages in releasing processes, consumption of litter by microorganisms and saprophages. Detailed description of the field methods and data processing has been presented earlier [5, 6].

Carbon and nitrogen were analysed by a gas chromatograph, Carlo Erba mod. 1102, cations were determined by a spectrophotometer of atomic absorption, phosphorus colorimetrically by the vanadium-molybdenum method.

As it has already been noted, there are considerable differences in the nutrient content of falling litter between the two ecosystems. They result from the differences in nutrient utilization between the plant communities in these habitats. For example,

TABLE I

Annual release of macronutrients from decomposing litter in *Pino-Quercetum* and *Carici elongatae-Alnetum* (all acting factors)

	Nutrients	Leaf fall kg/ha	Accumulation on filters per year litter+faeces kg/ha	Release per year	
				kg/ha	%
Pino-Quercetum	C	1746.20	952.70	−793.50	−45.44
	N	37.75	47.42	+9.67	+25.62
	Ca	38.04	38.52	+0.48	+ 1.26
	Mg	6.28	2.54	−3.74	−59.55
	K	11.31	2.09	−9.22	−81.52
	Na	1.17	1.77	+0.60	+51.28
	P	3.29	2.56	−0.73	−22.19
				$\bar{x}$	−18.65
				SD	47.61
				SD/$\bar{x}$	2.55
Carici elongatae-Alnetum	C	2046.90	743.23	−1303.67	−63.69
	N	118.78	46.18	−72.60	−61.12
	Ca	71.31	39.40	−31.91	−44.75
	Mg	12.11	2.05	−10.06	−83.07
	K	11.37	0.84	−10.53	−92.61
	Na	1.54	1.10	−0.44	−28.57
	P	4.19	1.92	−2.27	−54.18
				$\bar{x}$	−61.14
				SD	21.82
				SD/$\bar{x}$	0.36

the C:N ratio of the falling litter in the oak-pine forest is 46.3, while 17.2 in the alderwood. Similarly, the C:Ca ratio of the oak-pine forest litter is 45.9, while the litter of the alderwood is more rich in calcium, the ratio being 28.7 .The content of N, Ca, Mg, K, Na and P in the litter of the oak-pine forest is 2.8%, and in the litter of the alderwood it is 5.4% or twice higher.

Table I shows that the rate of nutrients release in the oak-pine forest is considerably lower than in the alderwood. In the former the mean annual release rate is about 19%, while in the latter about 61%. The second characteristic feature is a disproportion in the rate of nutrient release in the oak-pine forest, as compared with that in the alderwood. Some nutrients are released at a high rate, almost like in the alderwood (K, Mg). Others, such as Na, Ca, N, are not released at all during the annual cycle of litter decomposition, and they are accumulated. In the alderwood all macronutrients are released rapidly and relatively proportionally (Table I, Fig. 1). This regularity is best characterized by the ratio of the standard deviation

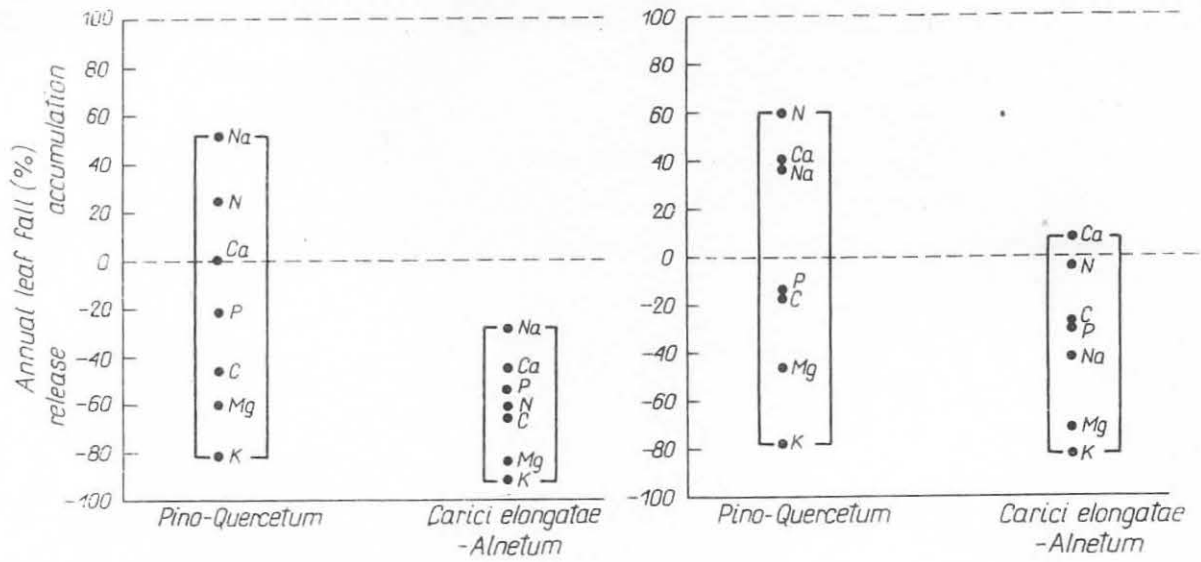

Fig. 1. Annual release of macronutrients caused by all acting factors (left) and by litter microorganisms (right) in *Pino-Quercetum* and *Carici elongatae-Alnetum*

to mean value. It is considerably higher in the oak-pine forest than in the alderwood (Table I).

It has been found that the release of nutrients from litter has two phases and each of them is controlled by different factors [6]. In the first phase the nutrients are released from morphic litter and this process is controlled by litter microorganisms, with water as a supplementary factor. In the second phase litter is decomposed from a morphic to amorphous form of highly comminuted faeces, and this process is controlled by saprophages, initiating litter decomposition, and such groups as microorganisms, coprophages, and even predators due to their consumption of lower trophic levels.

The macronutrient release in phase I is shown in Table II and Fig. 1. In the oak-pine forest it is very diversified. Some nutrients, such as K and Mg, are rapidly released from morphic litter, while such nutrients as N, Ca and Na are not released

but even accumulated in large amounts, up to 40—60% of the original content in morphic litter, due to the action of litter microorganisms.

The release of nutrients in the alderwood has a different pattern. The accumulation of nutrients is very limited. Only calcium is accumulated during the annual cycle, and in considerably smaller amounts than in the oak-pine forest. The other nutrients are relased from morphic litter. Therefore, the ratio of the standard deviation to the mean value, which characterizes the release of nutrients from morphic litter, has lower values in the alderwood than in the oak-pine forest (Table II).

The differences in the release of nutrients from morphic litter between the two ecosystems are best characterized by a dynamic analysis, which is presented for N, Ca and K in the annual cycle. Nitrogen and calcium are accumulated in the litter of the oak-pine forest, therefore, the annual balance of these nutrients is positive and litter is enriched in a dozen or so kilograms of these nutrients per hectar, as compared with the original content. In the alderwood the phase of nitrogen and calcium accumulation is very short, and it is followed by a rapid release of these nutrients. At the end of the annual cycle, nitrogen has a negative balance and several kilograms of it are released. Calcium is so rapidly accumulated in phase I that, although it is rapidly released afterwards, several kilograms per ha are accumulated during the annual cycle, which represents, however, only 8% of the original content. As for potassium, this nutrient is not accumulated and in both the communities it is rapidly released from morphic litter, Fig. 2, mainly due to abiotic leaching [1, 6].

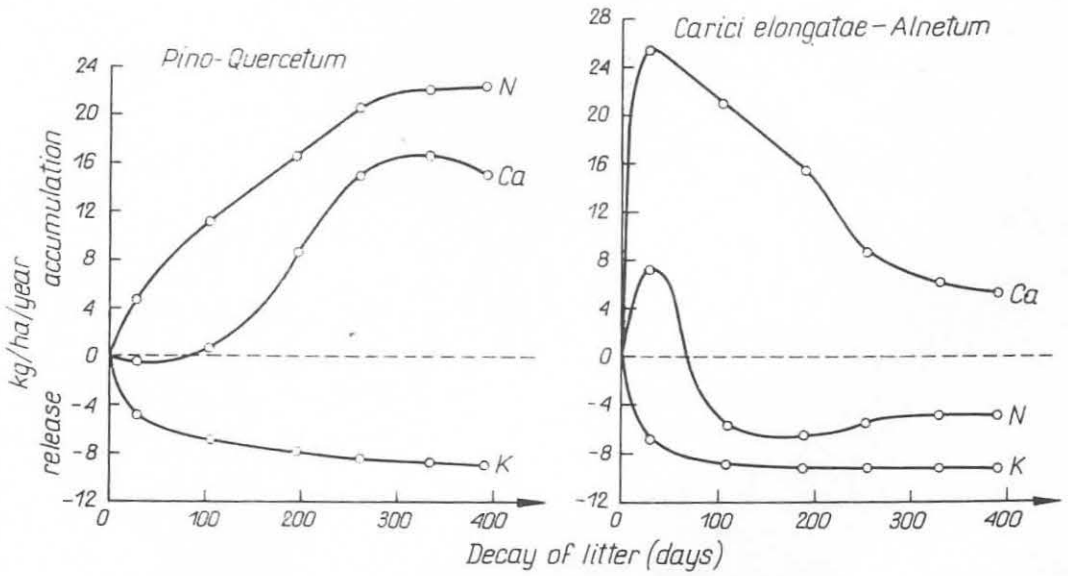

Fig. 2. Cumulative annual balance of N, Ca and K release or accumulation in the morphic litter of *Pino-Quercetum* and *Carici elongatae-Alnetum* in kg/ha/year

The presented facts indicate that the release of nutrients from the morphic litter of the oak-pine forest follows two patterns: some nutrients are rapidly released, the other are accumulated. In the alderwood the controlling factors, i.e., microorganisms and water, act much more uniformly in this phase of decomposition. Accumulation processes are reduced and the processes of release predominate.

The release of macronutrients in phase II, when litter is transformed into an amorphous substance, controlled by saprophages initiating the breakdown of litter, is characterized below. In the oak-pine forest such nutrients as K, Mg and Na are released at a relatively low rate (sodium is even accumulated). But C, N and Ca, thus the nutrients accumulated in phase I, are released at a considerably higher rate. Nevertheless, the accumulation of N and Ca in miophic litter is so high in this habitat that the annual balance of these nutrients is positive. For example, microorganisms accumulate in morphic litter 22.38 kg N/ha per year, while 12.71 kg N/ha per year is released in the processes initiated by saprophages. So, during the annual cycle 9.67 kg N/ha are accumulated (Table II). But saprophages are responsible

TABLE III

Release of macronutrients by litter microorganisms and saprophages in *Pino-Quercetum* and *Carici elongatae-Alnetum*

	Nutrients	*Pino-Quercetum*		*Carici elongatae-Alnetum*	
		in kg/ha	in % of leaf fall	in kg/ha	in % of leaf fall
Microorganisms	C	−310.70	−17.8	−575.90	−28.1
	N	+22.38	+59.3	−4.71	−4.0
	Ca	+15.32	+40.3	+5.47	+7.7
	Mg	−2.90	−46.2	−8.59	−70.9
	K	−8.82	−78.0	−9.34	−82.1
	Na	+0.426	+36.4	−0.649	−42.1
	P	−0.46	−14.0	−1.22	−29.1
		$\bar{x}$	−2.86		−35.51
		SD	50.23		32.72
		SD/$\bar{x}$	11.56		0.92
Saprophages	C	−482.8	−27.6	−727.8	−35.6
	N	−12.71	−33.7	−67.89	−57.2
	Ca	−14.84	−39.0	−37.38	−52.4
	Mg	−0.84	−13.4	−1.47	−12.1
	K	−0.40	−3.5	−1.19	−10.5
	Na	+0.174	+14.9	+0.208	+13.5
	P	−0.27	−8.2	−1.05	−25.1

for a very important process of N and Ca release, thus they may be considered as a factor compensating the accumulation of these nutrients in morphic litter.

A similar pattern of the release of macronutrients in the second phase of decomposition is observed in the alderwood. N and Ca are relased very rapidly, C only at a little slower rate, K and Mg relatively slow, Na is not released at all (Table II).

The direct and indirect role of saprophages in the release of macronutrients is best shown as a percentage of the total annual release of particular nutrients in particular habitats. Saprophages are responsible for a complete or almost complete

release of Ca and N in the habitats under study 94—100% of the annual release. Also C and P are released in large amounts 30—61%, while K and Mg are slowly released 4—22%, and Na is not released (Table III).

TABLE III

Release of macronutrients during the transformation of morphic litter into amorphous faeces expressed as a percentage of the total release of particular nutrients per year

Plant community / Nutrients	*Pino-Quercetum*	*Carici elongatae--Alnetum*
N	100.0	93.5
Ca	100.0	100.0
C	60.8	55.8
P	37.0	46.3
Mg	22.5	14.6
K	4.3	11.3
Na	accumulation	accumulation

Thus, saprophages release or initiate the release of N and Ca, while K, Mg and Na are mainly released without the contribution of animals, in the phase of morphic litter, when microorganisms and water are controlling factors.

As saprophages play a key role in the release rate of N and Ca, and also a considerable role in the release of C and P, it may be expected that the annual release of these nutrients largely depends on their consumption rate in the ecosystem. It has been found that both litter microorganisms and saprophages, which are the main consumers of litter, are much more active in the alderwood than in the oak pine forest (Table IV).

TABLE IV

Characteristics of the activity of heterotrophs in *Pino-Quercetum* and *Carici elongatae-Alnetum*

Plant community	Leaf fall	Litter consumption by		Total consumption by heterotrophs	% consumption of leaf fall by heterotrophs
		microorganisms	saprophages		
	kcal/ha·10^{-4}				
Pino-Quercetum	1670.2	252.0	750.3	1002.3	60.0
Carici elongatae--Alnetum	2032.9	498.1	1382.0	1880.1	92.9

The fact of slower, on the average, and much more disproportionate release of macronutrients in the oak-pine forest seems to be understandable now. It depends on the character of the activity of litter microorganisms, which accounts for a marked accumulation of some nutrients (N, Ca). On the other hand, saprophages initiating and accelerating the release of a number of nutrients (N, Ca, C and F) are much less active in the detritus food chain. In the alderwood, however, the processes of macronutrient release are rapid and proportional due to a limited accumulation by litter microorganisms, their higher activity and a high activity of saprophages in the detritus chain.

In sum, the following sequence of relationships can be recognized:

1) Plant communities, due to their ability to withdraw nutrients or to enrich the falling leaves in nutrients, can control the chemical composition of recycled organic matter in the ecosystem.

2) The content of nutrients in the organic matter has an effect on the rate and direction of the activity of litter microorganisms (accumulation or release of nutrients). It also determines the activity of saprophages in the detritus food chain which are the factor initiating and accelerating the release of a number of nutrients.

3) Character of the activity of microorganisms, and the activity of saprophages in the detritus food determine the rate of macronutrient release in the ecosystem which can be rapid and proportional if the falling organic matter is rich in nutrients, or slower and less proportional if it is scarce in nutrients.

It seems that there is a relationship between the type of nutrient utilization by plant communities in an ecosystem and the processes of litter decomposition. Our results suggest that the positive correlation between the content of nitrogen in litter and the decomposition rate observed earlier in [2, 7, 8] is of broader significance. More rapid litter decomposition is coupled not only with an apparent disappearance of morphic litter, its transformation in an amorphous form, but also with a real acceleration of the release of a number of nutrients. This acceleration, which is an effect of saprophagous activity, results in the fact that the nutrients which are slowly released from litter (N, Ca, P) keep pace with the nutrients rapidly released (K and Mg), and the whole releasing process is more harmonious over the year.

It seems that saprophages not only break down the litter physically but also initiate the release of a number of nutrients, including N and Ca. This is indicated by the fact that ammonium and urea are released by numerous saprophagous groups, e. g., *Lumbricidae* [3], this role being rather expected, at least as far as nitrogen is concerned. This seems to be a good illustration of the concept that the efficient release of nutrients can be effected only in the presence of a number of heterotrophs, including animals, thus it depends on the trophic structure of the community. From the point of view of nutrient cycling, simplification of the structure, although it can account for an increase in the productivity of ecological systems, seems to be followed by a delay in nutrient release and by a considerable disproportion in these processes.

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А. Стахурски, Е. Зимка, **Освобождение макроэлементов из разлогающейся подстилки ассоциации *Pino-Quercetum* и *Carici elongatae-Alnetum*. Роль микроорганизмов из подстилки и сапрофагов в процессах освобождения**

Содержание. В работе анализировано закономерность освобождения макроэлементов из подстилки (C, N, Ca, Mg, Kr P, Na) в двух типах экосистем.: *Pino-Quercetum* — ассоциации передающей почве подстилку убогую элементами и *Carici elongatae-Alnetum* — ассоциации передающей подстилку трофически бофатую, Установлено, что в ассоциации смешанного леса освобождение макроэлементов из подстилки в среднем более медленное и имеет более диспропорциональный характер чем в ольшанике — часть биогенов освобождается очень быстро (K, Mg), другие же элементы освобождаются медленно (в случае N, Ca, Na наблюдается даже аккумулирование этих элементов в годовом цикле), Об этом решает с одной стороны характер воздействия стилковых микроорганизмов: большая аккумуляция (N, Ca, Na — когда опадающая органическая материя убогая биогенами, ограничение процессов аккумуляции в случае высокого трофизма подстилки; с другой стороны, сапрофаги инициирующие и ускоряющие освобождение ряда биогенозы (N, Ca, P, C) включаются (в меньшей степени) в цепь детрификации в ассоциации смешанного леса чем в ольшанике.